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Survival in adults of the water frog *Rana lessonae* and its hybridogenetic associate *Rana esculenta*

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Abstract: Using recent developments in capture–mark–recapture modelling, I analysed survival rates of adults of two species of water frogs, the parent species *Rana lessonae* and its sexual parasite, the hybrid *Rana esculenta*. Frogs were caught in four different breeding ponds between 1995 and 1998 and the effects of genotype (= species), sex, pond, and time on survival rates and recapture probabilities were tested. Survival rates were consistently higher in *R. lessonae* than in *R. esculenta*. Recapture probability was higher in males than in females. In both species, survival rates were constant during spring and summer and similar in all years of the investigation, average monthly survival rates being lower than those during autumn and winter. The variation in annual survival rates (72–84% for *R. lessonae* and 53–70% for *R. esculenta*) is probably caused by differences in winter survival rates. Capture–mark–recapture models cannot separate mortality and emigration and hence usually underestimate survival rates. To eliminate this source of error, I quantified emigration, which ranged from 0 to 29% at the four ponds. After correcting for these emigration rates, I found no differences in survival rates among the four ponds. The overall high survival rates of adult *R. lessonae* compared with *R. esculenta* partially compensate for the hybrid's initial reproductive advantage in terms of mating, fertility, and larval development and, hence, contribute to stabilising mixed populations.

Résumé : À l'aide de découvertes récentes en modélisation capture–marquage–recapture, les taux de survie des adultes ont pu être analysés chez deux espèces de grenouilles, l'espèce parent *Rana lessonae* et son parasite sexuel, l'hybride *Rana esculenta.* Des grenouilles de quatre étangs de reproduction ont été capturées entre 1995 et 1998 et les effets du génotype (l'espèce), du sexe, de l'étang et du temps sur la survie et les probabilités de recapture ont été testés. La survie de *R. lessonae* était systématiquement meilleure que celle de *R. esculenta.* La probabilité de recapture était plus élevée chez les mâles que chez les femelles. Chez les deux espèces, la survie au printemps et en été était constante et elle est restée la même pendant toutes les années de l'étude; la survie mensuelle moyenne y était plus faible qu'à l'automne et en hiver. La variation de la survie d'une année à l'autre (72–84 % chez *R. lessonae* et 53–70 % chez *R. esculenta*) est probablement attribuable à la variation de la survie en hiver. Les modèles de capture–marquage–recapture ne peuvent distinguer mortalité et émigration et, par conséquent, sous-estiment généralement les taux de survie. Pour éliminer cette source d'erreur, les taux d'émigration, qui allaient de 0 à 29 % dans les quatre étangs, ont été quantifiés. Après avoir tenu compte de ces taux d'émigration et apporté les corrections nécessaires, il n'y avait plus de différence de survie entre les quatre étangs. La survie généralement plus élevée chez les adultes de *R. lessonae* peut compenser partiellement l'avantage reproducteur initial des hybrides en ce qui a trait à l'accouplement à la fertilité et au développement larvaire, et, par le fait même, elle contribue à stabiliser les populations mixtes.

[Traduit par la Rédaction]

Introduction

Understanding fluctuation and regulatory processes in populations or defining life-history strategies requires information on mortality or survival rates. Besides fecundity, sex ratio of adults, mating success, and dispersal, mortality is one of the key factors that influence population dynamics. However, survival rates are difficult to estimate under field conditions, where time of death is often unknown and the probability of survival may vary with time, environment, sex, or genotype (Caughley 1977; Lebreton et al. 1993). The recent development of powerful capture–mark–recapture analyses provides the opportunity to model survival estimates more exactly if data on marked individuals in periodically monitored populations are available (Lebreton et al. 1992).

In this study I investigated survival rates of adults of *Rana lessonae* and its hybridogenetic associate *Rana esculenta*. My main goal was to better understand factors that may regulate the structure and dynamics of mixed populations of these water frogs and lead to the temporal stability of genotype ratios that has been observed in natural ponds (Berger 1983). In central Europe, *R. esculenta* (genotype LR), originally a hybrid between *R. lessonae* (LL) and *Rana ridibunda* (RR), excludes its L-genome premeiotically and produces only sperm and eggs of the clonally transmitted R-genome (Berger 1977, 1983; Graf and Polls Pelaz 1989; Günther 1990). Consequently, *R. esculenta* has to mate with *R. lessonae* to regain the excluded genome in each generation. In populations without *R. ridibunda*, the two interspecific matings (LL × LR and LR × LL) result in *R. esculenta*, whereas the two intraspecific matings result in either *R. lessonae* (LL × LL) or nonviable *R. ridibunda* tadpoles (RR × RR). This, plus the fact that *R. esculenta* is superior to *R. lessonae* in

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terms of female fecundity (Berger 1977; Berger and Uzzel 1980) and tadpole survival (Heusser and Blankenhorn 1973; Semlitsch and Reyer 1992*a*; Semlitsch 1993), gives the hybrid a competitive advantage over the parent species. Yet the composition of natural water frog populations in terms of species frequencies among adults seems to be quite stable over time (Berger 1983). Besides nonrandom mating (Abt and Reyer 1993; Bergen et al. 1997; Roesli and Reyer 2000; Som et al. 2000; Engeler and Reyer 2001), differential survival after metamorphosis could, to a certain extent, counterbalance the hybrid's initial advantage and allow *R. lessonae* to catch up with it in numbers. However, in contrast to the numerous studies on larval development and survivorship to metamorphosis (e.g., Wilbur 1980; Smith 1983; Riis 1991; Semlitsch and Reyer 1992*a*; Rowe and Dunson 1995), relatively little is known about dynamics after metamorphosis (Sjögren 1988, 1991; Berven 1990; Neveu 1991). Since water frogs are reported to live to 6 or even 12 years of age, depending on the region they come from (Günther 1990; Sjögren 1991), the influence of adult survival is not to be neglected, and information on mortality is needed to understand population processes in these species. Generally one would expect that in long-lived animals, survival rates and fluctuations in survival rates have a strong influence on population dynamics, while in animals that live only for a short time the reproduction rate is more important (Hughes 1990).

In this paper I test the prediction that adult survival rates must be higher in *R. lessonae* than in *R. esculenta* to balance the fitness advantages of the hybrid during the early stages of reproduction. In pursuing this goal I analyse capture–mark–recapture data from adult water frogs from 4 different ponds and investigate the effects of genotype (= species), sex, pond, and time on the animals' survival rates. Annual survival rates are broken down into spring and summer and autumn and winter rates (*i*) to test for a direct influence of breeding on survival and (*ii*) to determine at which time of year most mortality occurs in water frogs. In contrast to other capture–mark–recapture studies, I include emigration rates in my analysis. This allows greater precision in determining actual survival rates because capture–mark–recapture analysis alone cannot distinguish animals that emigrate from those that die (Zeng and Brown 1987).

Materials and methods

Study area and monitoring

I collected capture–mark–recapture data at four breeding ponds (1, 2, 3, and 4) near Zürich, Switzerland (Fig. 1), all located within 1 km^2. Three of them (1, 2, and 3) were within less than 350 m of each other and there were two additional ponds nearby (A and B). Pond 4 was separated from this group of ponds both by a greater distance (900–1200 m) and by a motor highway. East of this highway was agricultural land with some industrial buildings but there was no frog habitat within 5 km.

In 1995 and 1996 the focal ponds 1–4 were monitored every second week between May 1 and August 10, which included breeding time between May and early July. In 1997 and 1998 the ponds were monitored at least once during the breeding season. Frogs were caught during the night by hand while a flashlight beam was directed at their eyes. One of the nearby ponds (A) was surrounded by a fence equipped with pitfall traps on both sides. Traps were checked daily between March 15 and November 25 and weekly during the rest of the year in 1995 and in 1996 (for details see Holenweg Peter 1999). The other nearby pond (B) was very small and was used as a breeding site in 1995 only. I caught animals there occasionally in 1995 and 1996.

All animals ≥40 mm snout–vent length were sexed by the presence or absence of vocal-sac openings and identified to species, mostly via allozyme electrophoresis (Tunner 1973; Vogel 1973) because morphological parameters overlap in these two species (Pagano and Joly 1999). I marked them individually with passive integrated transponder (PIT) tags (Trovan ID 100, Pameda AG, Münchenstein, Switzerland; Sinsch 1992), which could be identified afterwards by a hand reader (Trovan LID 500). After handling they were released back into their pond of origin or on the opposite side of the fence (pond A). A snout–vent length of 40 mm was taken as the lower limit because (*i*) smaller males often did not yet have vocal sacs and (*ii*) smaller animals could not be marked individually with PIT tags for morphological reasons. All handling of frogs was in accordance with the principles of the Canadian Council on Animal Care and specific Swiss regulations. Permission to catch and mark frogs was given by the Kantonales Veterinäramt, Zürich (No. 132/94).

The emigration rate was calculated as the ratio of the number of frogs that were marked at a particular pond and then recaught at another pond to the total number of frogs recaught, rather than to the total number of marked animals (Holenweg Peter 2001). The latter would have underestimated the emigration rate because it includes all frogs that were caught just once and, hence, could have died or moved undetected. However, the emigration rates so calculated are probably still too low because there are other ponds farther north in the area that were not monitored and to which animals could have moved.

Modelling procedures

To model survival and test biological hypotheses regarding survival, I followed the approach outlined by Lebreton et al. (1992). Data from ponds 1–4 were organised into capture-history arrays (Burnham et al. 1987), based either on biweekly data from 1996 for calculating spring and summer survival rates or on annual data from 1995–1998, pooled over all catching events within each year, for calculating annual survival rates. This resulted in 7 capture events between May and August 1996 for estimating summer survival rates and 4 capture events between 1995 and 1998 for estimating annual survival rates. A final analysis of all capture events from May 1, 1995, to June 30, 1998 (regardless of the different time intervals between the single capture events), yielded an estimate of winter survival rates. Data were analysed using the program SURGE 5 (Lebreton et al. 1992; Pradel and Lebreton 1993; Cooch et al. 1996). This program does not require closed populations, but animals migrating within or between populations do lower estimates of the survival rate because the model cannot separate emigration from mortality. Conversely, immigrating animals will reduce the probability of recapture because the model cannot distinguish between animals that are newly arrived at the site and those that were there before but have not been caught.

To test whether my data met the assumption of the modelling approach, I used the pooled χ^2 statistics of TEST2 (which tests for the effect of marking) and TEST3 (which tests for differences in survival) in the program REL-CR (Cezilly et al. 1993), a modified version of the program RELEASE (Burnham et al. 1987). For this, I first assessed the goodness of fit (GOF) of the most complex model, which was the fully time dependent Cormack–Jolly–Seber (CJS) model. I started the model selection only if the CJS model fitted the data satisfactorily. This most complex CJS model allowed survival rate (ϕ) and recapture probability (p) to vary with genotype (g), sex (s), locality (L), time (t), and their interactions (i.e., $\phi_{g \cdot s \cdot L \cdot t}$, $p_{g \cdot s \cdot L \cdot t}$). The notation for the models follows Lebreton et al. (1992) (Table 1). I constructed different models using a hierarchi-

Fig. 1. Map of the study area, with locations of sampling ponds 1–4, A, and B.

cal approach and proceeded to more simply structured models by removing nonsignificant effects from the previous model.

In some cases a better model was constructed by recoding the constraining parameters (e.g., *sgl*, *t*(1), *t*(2), *t*(3); Table 1). All parameters used were coded in a binomial way; for example, females with "0," males with "1" and *R. esculenta* with "0," *R. lessonae* with "1." Therefore, the sex × genotype (*sg*) interaction alone meant differences between male *R. lessonae* (1 × 1) and female *R. lessonae* (0 × 1), female *R. esculenta* (0 × 0) and male *R. esculenta* (1 × 0). To test for a difference between female *R. lessonae* and all other animals, via a sex × genotype interaction, I had to recode sex (i.e., females with "1" and males with "0"). The decision to test simpler models by recoding a parameter was based on the strength of the plotted survival and recapture probabilities of the best model with no parameters recoded.

Model selection was based on Akaike's Information Criterion (AIC), which was calculated as the deviance plus twice the number of parameters estimated by the model. The model with the lowest AIC was the most parsimonious one, i.e., the one with the best balance between simplification and precision (Lebreton et al. 1992; Burnham et al. 1995). When two models had AICs differing by less than 1, I chose the model with the lowest number of parameters if they were not nested, whereas I used a classical likelihood-ratio test (LRT) for model selection if they were nested (see also Toïgo et al. 1997; Loison and Langvatn 1998). The χ^2 value of the LRT corresponds to the difference in deviance between two nested models, with the difference in parameter number of each model given as the degrees of freedom.

SURGE 5 (as well as SURGE 4) can only treat 8 groups at once. However, because I had data from 4 localities (*l*) on 2 genotypes (*g*) and 2 sexes (*s*), I needed to handle 16 groups. Thus, in a first step I performed the model selection for *R. lessonae* and *R. esculenta* separately (starting with $\phi_{s\cdot L\cdot t}$, $p_{s\cdot L\cdot t}$) and tested in both species whether or not survival rates differed among the ponds 1,

Table 1. Notation used in the capture–mark–recapture models.

	Meaning
Main parameter	
ϕ	Survival
p	Recapture probability
Subscript	
g	Genotype
L	Locality (4 different ponds)
s	Sex
t	Time
l	Locality or pond type (connected ponds 1, 2, and 3 versus pond 4; similar parameters at the 3 connected ponds)
(sgl)	Interaction between sex, genotype, and locality type in such a way that sex differs at the 3 connected ponds and genotype differs at pond 4
$t(1)$	This code and the following ones were used for the last model, where I had 8 captures for 1995, 6 for 1996, 2 for 1997, and 1 for 1998; it indicates constancy over time during 1995 and 1996 but not between years
$t(2)$	Constancy over time within 1995, 1996, and 1997 (same values)
$t(3)$	Time-dependent only "within" years (constant values for 1995, 1996, and 1997) compared with "between years" (constant value for 1995–1996 and 1996–1997)

2, and 3 (called connected ponds), which were located close together. In this way, the initial factor locality (4 ponds) could be decreased to two locality groups (ponds 1, 2, and 3 versus pond 4). Both genotypes and sexes and the two locality types (l) were tested in the same model (starting with $\phi_{g\cdot s\cdot l\cdot t}$, $p_{g\cdot s\cdot l\cdot t}$).

Results

In total, 861 *R. lessonae* and 1376 *R. esculenta* were caught at ponds 1–4 between May 1, 1995, and June 18, 1998. I marked 886 animals during the 8 capture events between May 1 and August 9, 1995, and 827 animals during 7 capture events between May 15 and August 8, 1996. Five hundred and twenty-four were marked between June 6 and 25, 1997 (2 capture events), and between June 4 and 18, 1998 (1 capture event). Approximately 30% of the animals were caught more than once.

Within spring and summer

Summer survival and recapture probability

Analysis of survival and recapture rates during spring and summer had to be restricted to 1 year because the CJS model fitted the data satisfactorily for 1996 ($\chi^2 = 97.5$, df = 94, $P = 0.382$) but not for 1995 ($\chi^2 = 139.7$, df = 90, $P < 0.001$). Separate analyses for *R. lessonae* and *R. esculenta* showed that survival rates did not differ between ponds 1, 2, and 3, therefore I pooled the data from the connected ponds and considered all animals migrating between them to be recaptures at the same site. The main steps in the model selection are shown in the Appendix, which also illustrates the general selection procedure used in all subsequent analyses. The final, most parsimonious model includes constant survival probability over time, which differs between the genotypes in pond 4, but not between those in the connected ponds, and time-dependent recapture probabilities that differ by sex ($\phi_{g\cdot l}$, p_{s+t}; model 11 in the Appendix; Fig. 2). Males were caught more easily than females in both years. At pond 4, *R. lessonae* had a higher survival rate than *R. esculenta*.

Correcting for dispersal

The survival probability calculated by SURGE (ϕ_{surge}) is equal to the true survival probability (ϕ_{true}) multiplied by the probability of staying at the pond (1 – emigration).

$$\phi_{surge} = \phi_{true}(1 - \text{emigration})$$

$$\phi_{true} = \phi_{surge}/(1 - \text{emigration})$$

Frogs were moving between ponds 1, 2, 3, A, and B, but I did not observe any migrations to or from pond 4. Thus, pond 4 seemed to hold a fairly closed population compared with the other ponds. Even though total isolation is unrealistic, the true survival rate was probably equal or close to the survival rate calculated by SURGE. For ponds 1, 2, and 3, I knew at least the migration rates to the neighbouring ponds A and B. During spring and summer 1996, 10 of 83 recaught *R. lessonae* and 3 of 119 *R. esculenta* left the connected ponds. The mean emigration rates over 2 weeks (the mean of the ratios of emigrating animals to animals recaught within 2 weeks) were 0.104 for *R. lessonae* and 0.023 for *R. esculenta*. Using these values as estimates of emigration rate, the true survival probabilities at the connected ponds were 0.81 ($\phi_{true} = 0.724/(1 - 0.104)$) for *R. lessonae* and 0.74 ($\phi_{true} = 0.724/(1 - 0.023)$) for *R. esculenta* (shown in italics in Fig. 2). Thus, the true summer survival rates were higher for *R. lessonae* than for *R. esculenta* at both localities: the connected ponds (0.81 ± 0.027 versus 0.74 ± 0.027) and pond 4 (0.85 ± 0.052 versus 0.72 ± 0.027).

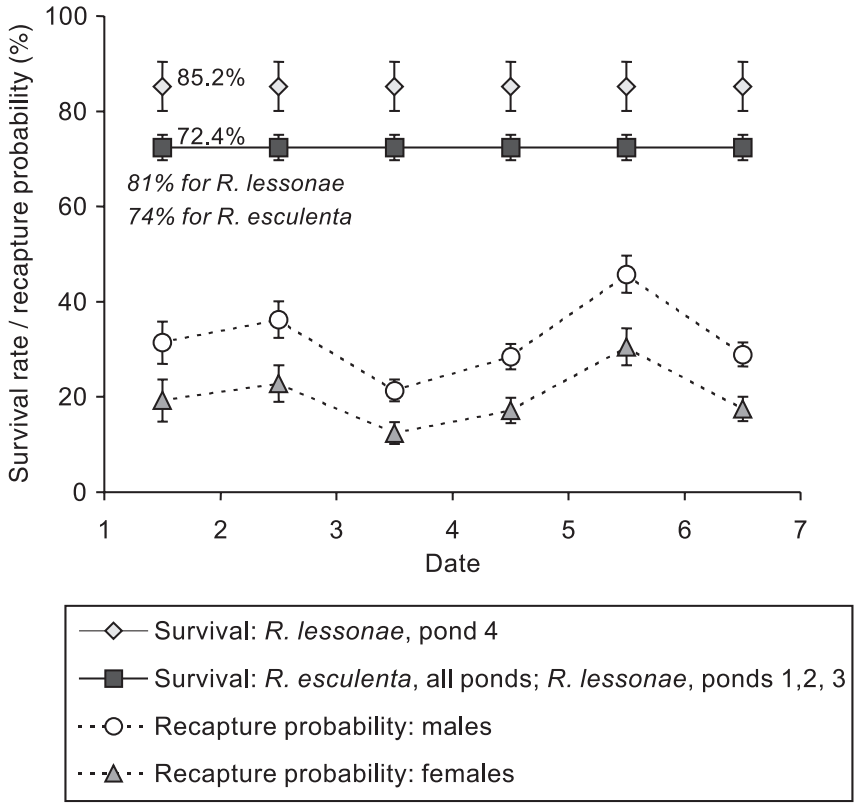
Between years

Annual survival and recapture probabilities

For analysing annual survival rates and recapture probabilities, I pooled the data within each year and combined the data from the connected ponds as I did before. This new data set met all assumptions of the CJS model ($\chi^2 = 28.3$, df = 21, $P = 0.132$).

The initial model-selection steps showed almost identical rates for males and females at pond 4 and for the genotypes at the connected ponds 1–3. Therefore, I recoded one parameter, allowing the genotypes to vary within pond 4 only and

Fig. 2. Survival rates and recapture probabilities (mean with standard deviation) at ponds 1, 2, 3, and 4 in 1996. The first capture date (date 1) was May 15 and the last capture date (date 7) was August 8, 1996. The numbers above the lines are calculated survival rates, including emigration rates; the numbers in italics reflect the true survival rates, corrected for dispersal.



the sexes to vary within the connected ponds (notation *sgl*). This best resulting model had constant survival rates that differed between females and males at the connected ponds and time-dependent survival rates that differed between the genotypes at pond 4 ($\phi_{(sgl)+tl}$, p_{t+sl}; Fig. 3). Between 1995 and 1996, 4 of 16 male and 5 of 17 female *R. lessonae* left the connected ponds and 1 of 37 male and 6 of 32 female *R. esculenta* did so. After correcting for this emigration, the true annual survival rates were 0.377 (ϕ_{true} = 0.283/(1 – 0.25)) for male and 0.212 (ϕ_{true} = 0.15/(1 – 0.294)) for female *R. lessonae*. For *R. esculenta* the corresponding values were 0.291 (ϕ_{true} = 0.283/(1 – 0.027)) for males and 0.185 (ϕ_{true} = 0.15/(1 – 0.188)) for females (shown in italics in Fig. 3). The recapture rates were time-dependent and higher for males at pond 4 than for the other animals.

Comparison between annual and summer survival rates

The annual survival rate includes the survival rate during spring and summer multiplied by the survival rate during autumn and winter (called the winter survival rate). In other words, the winter survival rate is the ratio between the annual survival and summer survival rates.

$$\phi_{annual} = \phi_{summer}^{(number\ of\ estimations)}\phi_{winter}$$

$$\phi_{winter} = \phi_{annual} \Big/ \phi_{summer}^{(number\ of\ estimations)}$$

At pond 4 in 1996 the calculated summer survival rate (0.852^6 for *R. lessonae* and 0.724^6 for *R. esculenta*) was already lower than the annual survival rate (1996 and 1997 in Fig. 3; 0.836 and 0.695, respectively). This would result in a winter survival rate higher than 1. There are two potential, and not mutually exclusive, explanations for this result. (1) Animals left this pond for another pond or wet area and were considered dead during spring and summer, but came back the following year. (2) Animals were hiding on land during spring and summer and were not recaptured before the following year. Observations on animals equipped with radio transmitters showed that they were really hiding not far from their ponds (A.-K. Holenweg Peter, unpublished data). Therefore, at pond 4 the true summer survival probability would be

$$\phi_{(summer)true} = \phi_{(summer)surge}/(1 - hiding)\ \text{and}$$

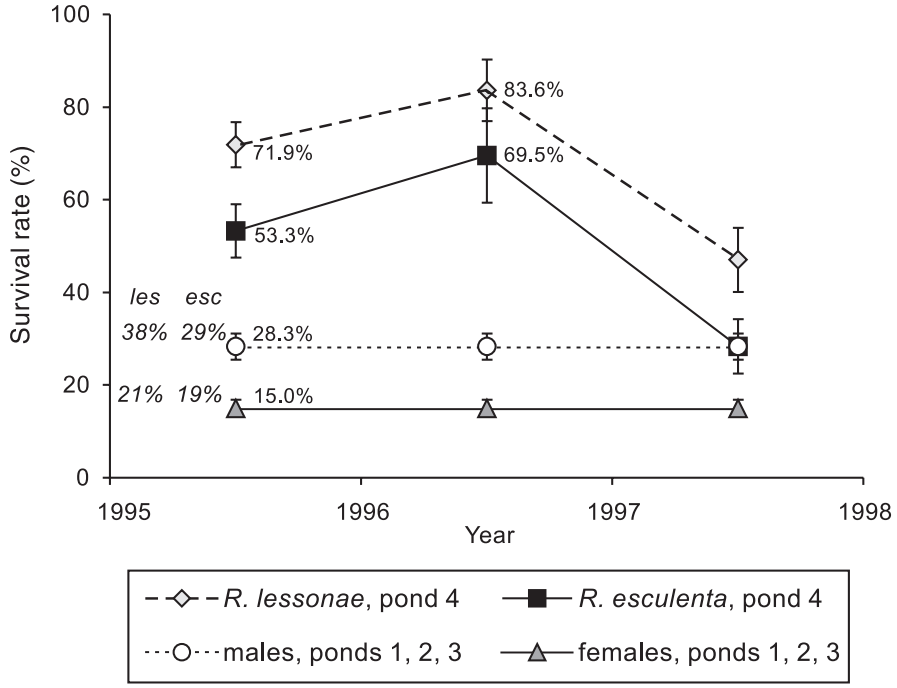
$$hiding = 1 - (\phi_{(summer)surge}/\phi_{(summer)true})$$

At the connected ponds 1–3 it would be

$$\phi_{(summer)true} = \phi_{(summer)surge}/(1 - emigration)(1 - hiding)$$

I estimated the probability that animals were hiding under two possible extreme scenarios: (1) survival in winter 1996–1997 was 1 or (2) survival in summer 1996 was 1. Such calculations can be problematic because an error may get larger, especially if the calculations are based on several assumptions. Therefore, I estimated the probability that animals were hiding only for pond 4, where no assumptions about emigration rates were required: (1) If the winter survival rate was 1 (ϕ_{winter} = 1), the true summer survival rate would equal the annual survival rate ($\phi_{(summer)true} = \phi_{annual}^{1/6}$), giving 0.971 for *R. lessonae* and 0.941 for *R. esculenta*. The resulting

Fig. 3. Annual survival rates (mean with standard deviation) from 1995 to 1998 at ponds 1, 2, and 3 in relation to sex and at pond 4 in relation to genotype ("*les*" is *R. lessonae*; "*esc*" is *R. esculenta*). The numbers beside the lines are calculated survival rates, including emigration rates; the numbers in italics reflect the true survival rates, corrected for dispersal.



hiding probabilities (hiding = $1 - (\phi_{(summer)surge}/\phi^{1/6}_{annual})$ would be 0.123 and 0.231, respectively. (2) If the summer survival rate was 1 ($\phi_{(summer)true} = 1$), the winter survival rate would equal the annual survival rate. The probability of hiding themselves would be 0.148 for *R. lessonae* and 0.276 for *R. esculenta* (hiding = $1 - \phi_{(summer)surge}$).

Winter survival

Winter survival rates and recapture probabilities

Both estimates of hiding do not differ much; however, they depend on the real winter survival rate. To obtain a more realistic estimate of winter survival, I analysed the data from 1995–1998 without pooling capture events and regardless of the different time intervals between capture events. I analysed all 17 capture events (the last capture in 1996 was omitted because the animals were not marked), starting on May 1, 1995, and ending on June 18, 1998. The CJS model fitted the data satisfactorily for pond 4 ($\chi^2 = 202.3$, df = 173, $P = 0.06$) but not for the connected ponds ($\chi^2 = 269.8$, df = 205, $P = 0.002$). These tests refer to the most complex model, which is based on a high number of degrees of freedom and sparse recapture data. Both factors enhance the chance of getting a significant GOF. Theoretically, this problem could have been solved by pooling some of the data (Lebreton et al. 1992). However, I refrained from doing so; instead, I only analysed data from pond 4 to avoid the problem of unknown migration rates at the other ponds.

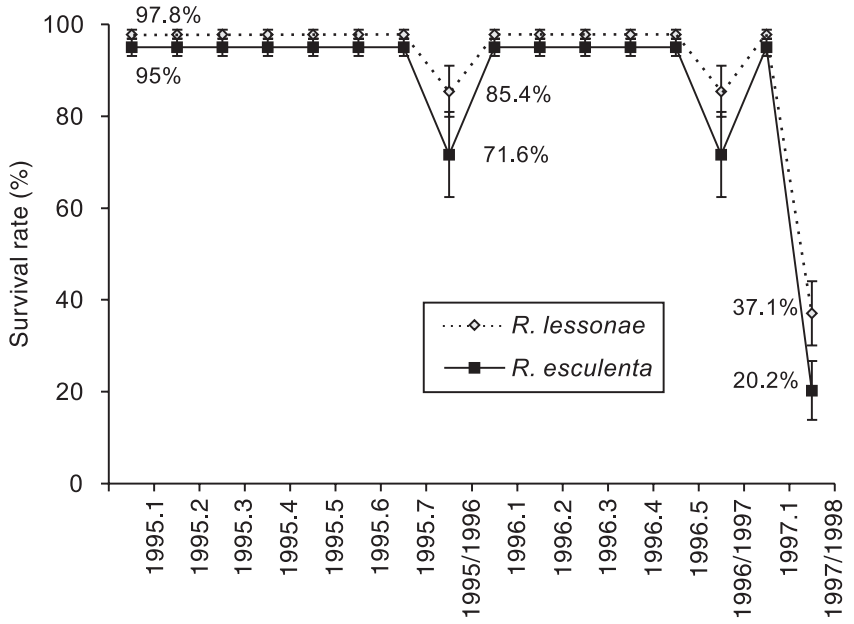
The best model showed a time-dependent survival probability, which was higher for *R. lessonae* than for *R. esculenta* (Fig. 4), and time-dependent recapture probability, which differed with time, genotype, genotype × sex, and sex × time. The model was further improved by simplifying the time dependence in such a way that survival rates were identical within the years 1995–1997 on the one hand and between years 1995–1996 and 1996–1997 on the other.

Nevertheless, not all of these survival rates can be compared directly, because they refer to different time intervals. The biweekly summer survival probability was 0.978 for *R. lessonae* and 0.950 for *R. esculenta*; the values did not differ within the 3 years of investigation. These values reflect true summer survival rates, which result in hiding probabilities of 0.129 (1 – (0.852/0.978)) and 0.238 (1 – (0.724/0.950)) for *R. lessonae* and *R. esculenta*, respectively. The winter and autumn survival rate in 1995–1996 (from August 9, 1995, to May 15, 1996) was 0.854 for *R. lessonae* and 0.716 for *R. esculenta*. The corresponding values for the following year are based on a longer time interval (from July 27, 1996, to June 6, 1997). After adjusting them to the same period as in 1995–1996 (from August 9 to May 15), I obtained 0.903 for *R. lessonae* and 0.814 for *R. esculenta* in 1996–1997 (survival(1996-08-09 to 1997-05-15) = survival(1996-07-24 to 1997-06-06)/summer survival$^{2.5}$). The same calculation was done for 1997–1998, assuming that the summer survival rate was the same for all years of investigation. The corresponding values were 0.419 for *R. lessonae* and 0.269 for *R. esculenta* (survival(1997-08-09 to 1998-05-15) = survival(1997-06-25 to 1998-06-18)/summer survival$^{5.5}$). To make all data comparable I calculated the survival probability per month: 0.956 for *R. lessonae* and 0.903 for *R. esculenta* (0.984 and 0.967 in 1995–1996, 0.990 and 0.980 in 1996–1997, and 0.917 and 0.877 in 1997–1998, respectively). Thus, in 2 of 3 years, winter survival was even higher than summer survival.

Discussion

The annual survival rates calculated from my capture–

Fig. 4. Survival rates at pond 4 between May 1, 1995 and June 16, 1998. Capture events took place between May 1 and August 9 in 1995 and between May 15 and July 24 in 1996, June 6 in 1997, June 25 in 1998, and June 18 in 1998. The numbers beside the lines are calculated survival rates, including emigration rates.



mark–recapture data, 53–85%, are higher than estimates from other anuran studies (Ryser 1986; Breden 1988; Berven 1990; Kuhn 1994), including 11–51% reported for *R. lessonae* and *R. esculenta* (Sjögren 1988, 1991; Neveu 1996). However, most of these studies did not consider, or only partially considered, emigration rates and recapture probabilities. Realistic capture probabilities, which are usually much lower than 1, and emigrating animals lower the survival estimates. Hence, previously reported estimates are probably too low. Even the values I found in my study may underestimate survival rates, especially at the connected ponds 1, 2, and 3, for which only emigration to the closest neighbouring ponds A and B was taken into account. This problem of dispersal confounding survival estimates can only be circumvented by additionally measuring the age structure of the population. This, however, requires toe-clipping and skeletochronology, which I did not perform.

After correction for emigration, the true survival probabilities for adult water frogs did not differ among the investigated ponds. This result is not too surprising because all ponds are located within 1 km^2 and represent similar habitats: they lie in open fields, are no farther than 100 m from the edge of the forest, and are lined with bushes. Hence, they experience the same weather conditions and probably also the same predation pressure on adult water frogs. The main predators on adult water frogs are different birds and small mammals, i.e., fairly mobile animals that are not restricted to one particular pond.

Spring and summer survival rates

Survival rates during spring and summer (May–August) were constant over time, indicating that the mortality rate was not higher during the breeding season (between May and the beginning of July), when reproducing animals are probably more easily discovered by predators and eat less (Juszczyk 1952). Yet, owing to the fact that there were only a few capture events after the breeding season, later effects may have remained undetected, and one cannot be sure that breeding activity has no long-term consequences on an animal's survival.

After emigration is accounted for, *R. lessonae* survived better than *R. esculenta* in all investigated ponds. Analysis of capture–recapture data from one season only (Fig. 2 and the Appendix) showed lower survival rates than analysis of data from 4 years (Fig. 4). This can be explained if we assume that estimates of survival are lowered not only by emigration but also by hiding on land: animals that were hiding during one season, and therefore considered dead, "revived" (statistically speaking) when they were recaptured the next year.

Recapture probabilities varied with time and sex. Males were caught more easily than females, probably because they were easier to detect during breeding, owing to their striking displays, which include calling. The variation in time is unlikely to be biologically interesting; it reflects primarily the variation in effort that was put into catching the animals (i.e., the number of people who helped) and the variation in weather conditions that influenced capture success (i.e., temperature and humidity). This holds for all analyses.

Annual and winter survival rates

The annual survival rate seems to be higher at pond 4 than at the connected ponds, even after emigration rates are accounted for. This difference was probably not as large as it looks because annual rates of emigration from the connected ponds were probably underestimated for methodological and (or) biological reasons. In terms of method, the number of animals recaught the following year was lower than the number caught during spring and summer. As a result, only

a few missed emigrants change the emigration rate, and consequently also the survival rate, more drastically the following year than during summer. In terms of biology, dispersal to the unsampled ponds to the north of the study area might be more pronounced between successive years because higher humidity and rainfall in autumn than during summer allows migration over longer distances (Blab 1982; Holenweg Peter 1999). Survival in 1996 was better than in 1995 at pond 4 but not at the connected ponds 1–3 (Fig. 3). However, I do not know the emigration rates for the latter ponds between 1996 and 1997; therefore, it is not clear whether the survival rates at these ponds were really equal in the 2 years. These results and uncertainties illustrate the need for further investigation of dispersal over longer distances to obtain better estimates of the actual survival rates at the connected ponds, whereas the calculated values at pond 4 are probably close to actual survival rates.

When data were pooled over all ponds and corrected for emigration, survival of *R. lessonae* was about 15% better per year than that of *R. esculenta*, and males survived better than females (ponds 1–3) or tended to do so (pond 4). This is consistent with the species and sex differences found by Neveu (1991) and Sjögren (1988, 1991), respectively.

Since summer survival rates were constant for all 3 years of the investigation, variation in annual survival rates was probably caused by differences in winter survival rates. The winter mortality rates of 6–18% (calculated for 6 months) were much smaller than the 30–40% suggested by Sjögren (1988). The average monthly survival rates during winter were higher than during summer, 98.7 versus 95.6% for *R. lessonae* and 97.4 versus 90.3% for *R. esculenta*. It seems that hibernation causes no high mortality rates in these cold-blooded animals, at least in the fairly moderate winter conditions that prevail at the latitude and altitude of my study site.

The low estimates of both annual (Fig. 3) and winter survival rates (Fig. 4) for the final year (1997–1998) are probably not correct. Since recapture probability was time-dependent and survival rate was partly time-dependent, their estimates could not be separated at the end of the study period (Lebreton et al. 1992; Cooch et al. 1996).

Conclusions

My analyses show that adult *R. lessonae* survive better than adult *R. esculenta* both during spring and summer and during autumn and winter. However, experiments with their tadpoles have shown the contrary: in most cases *R. esculenta* survived better than *R. lessonae* (Semlitsch and Reyer 1992*a*, 1992*b*; Semlitsch 1993). Survival data for the time during and after metamorphosis are scarce, but unpublished data from a field study by G. Abt indicate that *R. lessonae* survive better through metamorphosis than *R. esculenta*. The higher survival rates of *R. lessonae* during the adult and probably also the juvenile stages can counterbalance, to some extent, the reproductive advantage of *R. esculenta* during the early stages of reproduction (cf. Introduction). Hence, the higher survival rate among adult *R. lessonae* than among adult *R. esculenta* may be one of the key factors that contributes to stability in mixed *R. lessonae* – *R. esculenta* populations.

More generally, my study illustrates the importance of including migration rates, hiding rates, and capture probabilities in estimates of survival. These confounding factors will not only artificially lower true survival rates, they can also give the impression of differences in survival rates between localities, species, or sexes when, in fact, these groups only differ in behaviour and, hence, in capture probabilities.

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Appendix.

Model selection for survival and recapture probabilities within 1996; only the main steps are shown. For each model the number of estimable parameters, the relative deviance, and Akaike's Information Criterion (AIC) are given; ns, not significant. The final model is shown in boldface type.

Model	Parameter	Relative deviance	AIC
(1) $\phi_{g\cdot s\cdot l\cdot t}$, $p_{g\cdot s\cdot l\cdot t}$	87	1785.707	1959.707
(2) $\phi_{g\cdot s\cdot l\cdot t}$, $p_{g+s+l+t}$	57	1814.936	1928.936
(3) $\phi_{g\cdot s\cdot l\cdot t}$, p_{g+s+t}	56	1814.951	1926.951
(4) $\phi_{g\cdot s\cdot l\cdot t}$, p_{s+t}	55	1817.759	1927.759
→ Model 4 vs. model 3: △AIC < 1, χ^2 = 0.015, df = 2, ns			
(5) $\phi_{g\cdot s\cdot l\cdot t}$, p_s	50	1840.400	1940.400
(6) $\phi_{g\cdot s\cdot l\cdot t}$, p_t	54	1827.214	1935.214
(7) $\phi_{g+s+l+t+gl}$, p_{s+t}	17	1856.082	1890.082
(8) $\phi_{g+l+t+gl}$, p_{s+t}	16	1856.335	1888.335
→ Model 8 vs. model 7: △AIC < 1, χ^2 = 0.253, df = 1, ns			
(9) ϕ_{g+l+gl}, p_{s+t}	11	1858.334	1880.334
(10) ϕ_{g+gl}, p_{s+t}	10	1858.518	1878.518
(11) ϕ_{gl}, p_{s+t}	**9**	**1860.167**	**1878.167**
→ Model 11 vs. model 10: △AIC < 1, χ^2 = 1.649, df = 1, ns			
(12) ϕ_g, p_{s+t}	9	1865.276	1883.276
(13) ϕ, p_{s+t}	8	1865.356	1881.356